

Understanding clustering in type space using field theoretic techniques

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February 2, 2008

Abstract

The birth/death process with mutation describes the evolution of a population, and displays rich dynamics including clustering and fluctuations. We discuss an analytical ‘field-theoretical’ approach to the birth/death process, using a simple dimensional analysis argument to describe evolution as a ‘Super-Brownian Motion’ in the infinite population limit. The field theory technique provides corrections to this for large but finite population, and an exact description at arbitrary population size. This allows a characterisation of the difference between the evolution of a phenotype, for which strong local clustering is observed, and a genotype for which distributions are more dispersed. We describe the approach with sufficient detail for non-specialists.

Keywords: *neutral evolution, birth/death process, field theory, dimensional analysis, stochastic partial differential equation, PDE*

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1 Introduction

Throughout the biological literature, the term “diffusion in genotype space” is used to describe a population acting under genetic drift in the absence of selection. This is not diffusion at the *individual* level, but at the *population* level, where the individuals form clusters resembling a species, the mean position of which performs a random walk i.e. diffuses. The ‘species’ may consist of a number of clusters at any given time. However, these clusters remain close together, and the species is limited in the maximal width that it can achieve in any given direction in the space [1].

Clustering phenomena are well understood for reproducing and dying organisms dispersing in real space [2, 3]. In the case of real space, the relationship of the microscopic process to the stochastic Partial Differential Equation (PDE) formalism is clear, due to the (exact) field theory mapping [4] of the underlying microscopic process to a stochastic PDE. However, no such translation has been done in the case of type (sequence) space, be it of a genotype or a phenotype, where clustering phenomena are also observed [1, 5, 6]. We perform the translation and show that reproducing and dying organisms either diffusing in real space or mutating in type space are fundamentally the same process in an infinite population. This equivalence only applies in the infinite population limit, and so we provide finite size corrections to the stochastic PDE, allowing for individuals to mutate only on a birth event.

From known results for diffusing organisms, there exists an ‘upper-critical dimension’ d_c , above which general ‘mean field’ results hold but below which the behaviour is different. A phenotype forms a one dimensional type space, which can be thought of as a single trait. Conversely, we consider a genotype as a very long amino acid string, and hence genotype space is high dimensional as mutations are free to occur at a large number of independent positions.

28 Therefore there exists an important distinction between the evolution of a given
 29 phenotype, and a genotype. The theory of Critical Branching Processes [7] finds
 30 that in high dimensions describing genotype space ($d > d_c$, where in our case the
 31 critical dimension $d_c = 2$ [8]), birth/death dynamics are described fully by the
 32 lineages. A lineage remains distinct until all individuals in it die. However, in
 33 low dimensions ($d \leq d_c$) describing a particular phenotype, additional clustering
 34 within the distribution of the lineage occurs. Although sometimes distinct, the
 35 clusters in phenotype space can merge, and hence clusters are poorly defined
 36 entities. Instead, a careful average over the distribution called a ‘peak’ provides
 37 a more useful description of phenotypes [1].

38 Critical Branching Processes have a total population that does a random
 39 walk and only surviving lineages with $N(t_{final}) > 0$ are considered. For real
 40 space birth/death processes, the same phenomenological clustering and upper-
 41 critical dimension $d_c = 2$ are also found when considering systems of fixed
 42 population size [9]. As we show that neutral evolution has the same description
 43 in the infinite population limit as Critical Branching Processes in real space,
 44 this result also applies to evolution, and for qualitative studies we can choose
 45 whether to consider systems of fixed or fluctuating total population.

46 We use the technique of second quantisation of a master equation and map-
 47 ping to a field theory[4], for which most previous work focuses on the infinite
 48 population limit. However, field theory is a good tool for obtaining analytical
 49 results for finite and changing population sizes, as is the case for real popula-
 50 tions. The technique was developed in the setting of reaction-diffusion systems,
 51 where particles diffuse continuously, unlike our case of diffusion in a type space
 52 *where the diffusion only occurs on a birth or death event.*

53 This paper addresses three main issues:

- 54 1. We discuss how a microscopic model of evolution can be represented as a

- 55 Field Theory, and derive the stochastic PDE that follows in this case.
- 56 2. Understanding the ‘asymptotic’ behaviour, i.e. the infinite population
57 and long wavelength properties of evolution, by identifying that this is a
58 solved problem. Super Brownian Motion and Critical Branching Processes
59 provide a wealth of results which are made explicit by the comparison of
60 the relevant stochastic PDEs.
- 61 3. Relating the asymptotic behaviour to the behaviour at finite population
62 size.

63 1.1 Known results for clustering due to birth/death pro- 64 cesses

65 We will use known results of birth/death processes from the field of Critical
66 Branching Processes, which tackles similar problems to field theory techniques
67 but differs in approach and terminology. Refs. [7] and [8] give more details, and
68 a more direct technique is used in [9].

69 As discussed above, the behaviour is qualitatively different above and be-
70 low a critical dimension d_c . In the language of statistics, for $d \leq d_c$ the only
71 stable solution is a δ_0 measure in the correlations between individuals - i.e. all
72 individuals are fully correlated in their position. This implies that all individ-
73 uals are localised in space so that their distribution collapses to a point when
74 viewed at very large length-scales. In unscaled type space, this corresponds to
75 a local peak *with a characteristic width* (s) i.e. a length-scale. The length-scale
76 s scales to 0 in the infinite population limit for $d \leq d_c$. However, for $d > d_c$
77 other non-trivial measures exist describing the correlations in the system, which
78 correspond to a distribution of individuals spread out over a number of lineages.
79 The distribution of time since last ancestor forms a power-law distribution in
80 the infinite population limit, and since lineages typically do not intersect in high

81 dimensions, there is no characteristic width to the distribution (and hence no
82 length-scale).

83 The theorems available for the clustering process are usually devoted to
84 deriving general behavioural properties, such as the convergence to either of
85 the above measures in various dimensions. Many clustering phenomena are
86 described by the same scaling relations for $d > d_c^i$, where i is a label for a
87 particular phenomena (e.g. birth/death processes in Euclidean space, as our
88 model). Thus each model may have a different critical dimension, but above
89 that the scaling behaviour is the same. Examples are given in [7]: Galton
90 Watson Trees embedded into space (which is the real space diffusion version
91 of our model) have $d_c = 2$, Directed Percolation [4] has $d_c = 4$, Percolation
92 has $d_c = 6$ and Lattice Trees (a lineage tree embedded in a lattice so that
93 separate lineages never meet) have $d_c = 8$. All dimensions refer to the number
94 of spatial dimensions - the stochastic process consists of the extra dimension of
95 time. Below the critical dimension each model behaves specially, however above
96 the critical dimension all models follow the same scaling relation. All of these
97 models can be described as a birth/death process embedded in some type of
98 space.

99 Super Brownian Motion is the limiting process of all of the above processes
100 for $d > d_c$. This can be described by a stochastic PDE in many cases. In the
101 case of Galton-Watson Trees [10], in terms of the density ρ as a function of space
102 x and time t , the stochastic PDE is:

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = D \nabla^2 \rho(\mathbf{x}, t) + c \sqrt{\rho(\mathbf{x}, t)} \eta(\mathbf{x}, t), \quad (1)$$

103 where D is the diffusion constant and c is a constant describing the magnitude
104 of the noise. We will obtain this functional form in the infinite population limit
105 for the case of evolution in type space, which with some dimensional analysis

106 means that evolution as we define it has $d_c = 2$.

107 1.2 The model

108 We consider $N(t)$ individuals at time t , and each individual has a discrete type
109 $x \in \mathcal{Z}^d$, which it *retains during its lifetime*. The dimension of type space d is ar-
110 bitrary in the formalism. A timestep consists of performing a birth attempt with
111 probability $p_{off}/(p_{off} + p_{kill})$, or otherwise a killing attempt occurs*. We focus
112 on the case $p_{kill} = p_{off}$ throughout this discussion. Time is measured in genera-
113 tions and increases by the average waiting time between events, $1/N(p_{off} + p_{kill})$
114 per timestep.

- 115 • Birth attempt: A parent individual (with type x) is selected at random,
116 and an offspring is created with type x and mutated with probability p_m .
117 A mutation involves x changing by ± 1 in a randomly chosen direction.
- 118 • Killing attempt: A randomly chosen individual is removed.

119 This definition differs from the case of a birth/death process with diffusion
120 in real space, where all individuals are diffusing constantly between birth/death
121 events. Our model permits ‘diffusion’ only on birth events via mutation. A
122 sample run is shown in Figure (1) for an early and late time, and a sample
123 distribution from diffusion is shown for comparison. Simulations at different
124 N show that there is a clustering behaviour that persists regardless of N (not
125 shown, though see [1]). We wish to understand how the clustering depends on
126 dimensionality, both qualitatively and quantitatively.

*This is an example of the Gillespie algorithm [11].

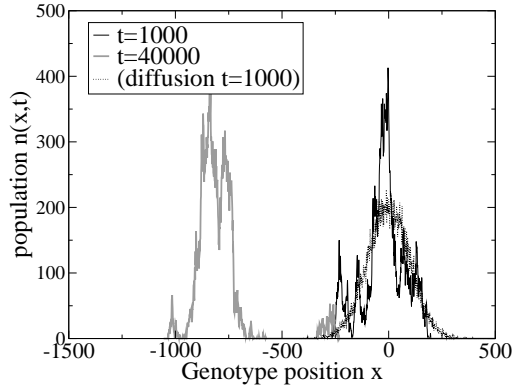


Figure 1: Sample distribution for $N = 10000$ individuals starting at 0 and evolving in a 1-dimensional type space. For early time, (black line) the distribution behaves similarly to diffusion, but once the peak has become ‘large’, it begins to move around, and can split up into a number of clusters (as shown by grey line). The distribution for $N = 10000$ diffusing particles [1] is also shown (a normal like distribution centred at zero, dotted line) at early time; the width increases as \sqrt{t} .

2 Field theory approach to obtain a Stochastic PDE

Doi’s process of second quantisation [12] is used to obtain a Field Theory from a Master Equation. A detailed description of the mapping process is presented in [4], and a detailed background can be obtained from [13].

2.1 Outline of the method

We outline the method for obtaining a field theory from a Master Equation of the form $dP(\{n\}, t)/dt = f(\{n\})$. Here $P(\{n\}, t)$ is the probability distribution of the state $\{n\} = \{n_1, \dots, n_i, \dots, n_L\}$, where L is the size of the type space and n_i is the population size of a given type i .

1. Define the state $|\{n\}\rangle$, and use the equation for $dP(\{n\}, t)/dt$ to obtain an equation of motion for $|\{n\}\rangle$.

- 139 2. Define $|\{\phi\}\rangle$ as the superposition of all possible states with probabilities
140 $P(\{n\}, t)$. This provides an equation of motion of the form $d|\{\phi\}\rangle/dt =$
141 $-\hat{H}|\{\phi\}\rangle$, where \hat{H} is called the *Hamiltonian*.
- 142 3. The state $|\{\phi\}\rangle$ is expressed in terms of operators; the field $\phi(\mathbf{x}, t)$ emerges
143 as a natural quantity in the system, being the eigenvalue of the so called
144 ‘creation’ operator, which counts the number of individuals and hence is
145 related to the density. The field $\phi(\mathbf{x}, t)$ is simply a complex number defined
146 for all spatial points x .
- 147 4. By taking the continuous space limit, the equations for $\phi(\mathbf{x}, t)$ become
148 tractable.
- 149 5. Observables \overline{A} can be related to ϕ in terms of functional integrals. How-
150 ever, most quantities of interest such as the density can be obtained di-
151 rectly from examination of the Hamiltonian alone.
- 152 6. A stochastic PDE in our case can easily be obtained from H , providing
153 access to other techniques or, in our case, previous results.

154 We find that additional terms appear in the field theory due to the insis-
155 tence that movement only occurs on a birth; these are difficult to deal with
156 in analytical calculations. These terms are negligible in the infinite population
157 limit, in which case our model reduces to the real space birth/death process
158 with diffusion of individuals. This is a previously solved case, as discussed in
159 Section 1.1. We are also concerned with the finite population case, for which
160 we provide both an exact and an approximate stochastic PDE.

161 2.2 To Second Quantised form

We now follow the procedure of second quantisation of a Master Equation, providing explicit details only for the one-dimensional case for readability. The

starting point is the master equation for the Evolution process as defined above. The equation for the change in the probability distribution $p(\{n\})$ over all sites $\{n\} = (n_1, \dots, n_i, \dots, n_{L-1}, n_L) \equiv n_i$, in notation enumerating only sites different from $\{n\}$ for brevity, is:

$$\begin{aligned} \Delta_t p(n_i; t) = & \\ & \frac{p_{off}}{2N} \sum_i \left\{ n_i [p_m p(n_{i-1} - 1; t) + p_m p(n_{i+1} - 1; t) - 2p(n_i; t)] \right. \\ & + 2(1 - p_m)(n_i - 1)p(n_i - 1; t) \\ & \left. + 2(n_i + 1)p(n_i + 1; t) - 2n_i p(n_i; t) \right\}. \end{aligned} \quad (2)$$

Eq. (2) follows directly from a microscopic description of the model. We sum over all possible lattice points i where a change could occur. The terms from left to right are, on the top line: enter state $\{n\}$ by a birth at i mutating left; mutating right; leaving state $\{n\}$ by a birth at i . Second line: entering state $\{n\}$ by a birth without mutation. Third line: entering state $\{n\}$ by a death at i , and leaving state $\{n\}$ by a death at i . We have ignored boundary terms as we will take $L \rightarrow \infty$.

The state $|n_i\rangle$ of a lattice point i is defined as the number of individuals on it. We then define the state of the system $|\{n\}\rangle = |n_1\rangle \otimes \dots \otimes |n_L\rangle$, where \otimes denotes the outer product.

Eq. (2) is multiplied by $|\{n\}\rangle$, and we then relabel the states within the sum to ensure that the probabilities in all terms are expressed in terms of $p(\{n\})$, allowing the ‘state’ vector to become different from $|\{n\}\rangle$. Then we can define operators acting on the state in order to recover all terms in the summed state $|\{n\}\rangle$. These operators also capture multiplicative terms in the number of individuals n_i . We define the operators, called the annihilation operator \hat{a} and the creation operator \hat{a}^\dagger , by their commutation relations:

$$[\hat{a}_i, \hat{a}_j^\dagger] = \delta_{ij}, \quad (3)$$

$$[\hat{a}_i, \hat{a}_j] = [\hat{a}_i^\dagger, \hat{a}_j^\dagger] = 0. \quad (4)$$

179 The notation $[\hat{a}_i, \hat{a}_j^\dagger]$ means simply $\hat{a}_i \hat{a}_j^\dagger - \hat{a}_j^\dagger \hat{a}_i$. If we define the ‘vacuum lattice’
 180 $|0\rangle$ by $\hat{a}_i |0\rangle = 0$ for all i , and $|n_i\rangle = (\hat{a}_i^\dagger)^{n_i} |0\rangle$ then it is simple to show that the
 181 operators follow:

$$\hat{a}_i |n_i\rangle = n_i |n_i - 1\rangle, \quad (5)$$

$$\hat{a}_i^\dagger |n_i\rangle = |n_i + 1\rangle. \quad (6)$$

182 On multiplication of Eq. (2) by the state $|\{n\}\rangle$, summation over all states $\{n\}$,
 183 performing the relabelling and using the creation and annihilation operators,
 184 we find:

$$\begin{aligned} \Delta_t \sum_{\{n\}} p(\{n\}; t) |\{n\}\rangle &= \frac{p_{off}}{2N} \sum_{\{n\}} \sum_i p(\{n\}; t) \left\{ p_m \hat{a}_{i-1}^\dagger \hat{a}_i^\dagger \hat{a}_i + p_m \hat{a}_{i-1}^\dagger \hat{a}_i^\dagger \hat{a}_i - 2\hat{a}_i^\dagger \hat{a}_i \right. \\ &\quad \left. + 2(1 - p_m)(\hat{a}_i^\dagger)^2 \hat{a}_i + 2\hat{a}_i - 2\hat{a}_i^\dagger \hat{a}_i \right\} |\{n\}\rangle, \end{aligned} \quad (7)$$

185 Or we can write this in (quasi)Hamiltonian form, using the notation $|\{\phi\}\rangle =$
 186 $\sum_{\{n\}} p(\{n\}; t) |\{n\}\rangle$:

$$\Delta_t |\{\phi\}\rangle = -\hat{H} |\{\phi\}\rangle, \quad (8)$$

187 with the Hamiltonian:

$$\hat{H} = \frac{p_{off}}{2N} \sum_i \left[-p_m(a_{i-1}^\dagger + a_{i+1}^\dagger - 2a_i^\dagger)a_i^\dagger a_i - 2(a_i^\dagger - 1)^2 a_i \right]. \quad (9)$$

188 This completes the mapping to second-quantised form.

189 2.3 From Second Quantisation to Field Theory

190 The next step involves constructing so called ‘coherent states’ such that $\hat{a}_i|\phi\rangle =$
 191 $\phi_i|\phi\rangle$, and $\langle\phi|\hat{a}_i^\dagger = \langle\phi|\phi_i^*$ as described in [4]. The eigenvalues ϕ_i and ϕ_i^* of
 192 the \hat{a} and \hat{a}^\dagger operators respectively are complex numbers at a given point, and
 193 therefore in the continuous limit form a *field* ϕ in space x . This allows one
 194 to calculate observables by use of a projection state. Here we simply use the
 195 results that $\hat{a}_i \rightarrow \phi_i$, $\hat{a}_i^\dagger \rightarrow \phi_i^*$. The continuous limit is then taken by allowing
 196 $\sum_i \rightarrow \int h^{-1}dx$, $\phi_i \rightarrow \phi(\mathbf{x}, t)h$ and $\phi_i^* \rightarrow \tilde{\phi}(\mathbf{x}, t)$, where we take h (the distance
 197 between lattice points) to zero. It can be shown that $\langle\phi\rangle = \langle n(\mathbf{x}, t)/N \rangle$. We
 198 consider the $\tilde{\phi}(\mathbf{x}, t)$ and $\phi(\mathbf{x}, t)$ fields to be independent. This completes the
 199 mapping to a field theory, in terms of the *Action* in the Statistical Weight:

$$S[\tilde{\phi}, \phi] = \int d^d x \left\{ -\phi(t_f) - \tilde{\phi}(0)[1 - \bar{n}_0] + \int_0^{t_f} [\tilde{\phi}\partial_t\phi + H(\phi, \tilde{\phi})] dt \right\}, \quad (10)$$

200 expressed in terms of final time t_f , and the average initial occupancy \bar{n}_0 . The
 201 Action is related to the expectation of an observable A by:

$$\overline{A}(t) = \mathcal{N}^{-1} \int \left(\lim_{L \rightarrow \infty} \prod_{i=1}^L \mathcal{D}\phi_i \mathcal{D}\phi_i^* \right) A(\{\phi\}_t) \exp[-S(\{\phi^*\}, \{\phi\})_0^t]. \quad (11)$$

202 We have introduced a normalisation factor \mathcal{N} and the path integral notation
 203 $\mathcal{D}\phi_i$ [4]. Path integrals of the form of Eq. (11) have been well studied and we will
 204 discuss some of methods available to avoid performing explicit integration, by

205 considering the Action S directly. The Action depends only on the Hamiltonian
 206 which we have derived from the Master Equation above. Following this process
 207 for our case of neutral evolution from Eq. (9) we have:

$$H(\phi, \phi^*) = \frac{p_{off}}{2N} \sum_i [-p_m(\phi_{i-1}^* + \phi_{i+1}^* - 2\phi_i^*)\phi_i^*\phi_i - 2(\phi_i^* - 1)^2\phi_i], \quad (12)$$

208 or in the continuum limit:

$$H(\phi, \tilde{\phi}) = D \int d^d x \left[-(\nabla^2 \tilde{\phi}(\mathbf{x}, t))\tilde{\phi}(\mathbf{x}, t)\phi(\mathbf{x}, t) - \frac{2}{p_m}(\tilde{\phi}(\mathbf{x}, t) - 1)^2\phi(\mathbf{x}, t) \right]. \quad (13)$$

209 We have introduced the Diffusion Constant $D = (p_{off}p_m/2)(h^2/Ndt)$, which is
 210 kept constant when taking the limit. The distance between types is h and dt is
 211 the timestep. This equation is recovered for any dimensionality of Eq. (2). We
 212 will use the notation $\phi(\mathbf{x}, t) = \phi$ where this is unambiguous.

213 The ‘classical solution’ to Eq. (13) is obtained by considering only terms at
 214 most bilinear in ϕ and $\tilde{\phi}$, corresponding to the noiseless case. This has $\tilde{\phi} = 1$,
 215 as is easily checked using the methods from Section 2.6. Therefore it is useful
 216 to perform a field shift $\tilde{\phi} \rightarrow \bar{\phi} + 1$ to obtain a neater Hamiltonian:

$$H(\phi, \bar{\phi}) = D \int d^d x \left[-\bar{\phi} \nabla^2 \phi - \phi \bar{\phi} \nabla^2 \bar{\phi} - \frac{2}{p_m} \bar{\phi}^2 \phi \right]. \quad (14)$$

217 The variable we are working with here, ϕ , does not correspond directly to the
 218 real density we measure, although the expectation value for the two is the same.
 219 The density [14] is $\tilde{\phi}\phi = \rho$, which can be obtained directly by defining $\tilde{\phi} = e^{\bar{\rho}}$,
 220 and $\phi = \rho e^{-\bar{\rho}}$; ρ is a real valued field. This allows us to obtain an explicit
 221 equation for the density; however, the exponentials must be considered as their

sum expansion, and in our case they do not cancel. We will later be able to show that the higher order terms are progressively less important when the population is large. Writing the less important terms within sums, the Hamiltonian for the real density for evolution in a type space is therefore:

$$H(\rho, \tilde{\rho}) = \int d^d x \left(-D\tilde{\rho} \nabla^2 \rho - \frac{2D}{p_m} \rho \tilde{\rho}^2 - D \sum_{n=2}^{\infty} \frac{\tilde{\rho}^n}{n!} \nabla^2 \rho - \frac{4D}{p_m} \sum_{m=2}^{\infty} \frac{\tilde{\rho}^{2m}}{(2m)!} \rho \right). \quad (15)$$

We will use two different Hamiltonians in the following analysis, $H(\phi, \bar{\phi})$ for the complex field, and $H(\rho, \tilde{\rho})$ for the real density field. Note that the over-line $\bar{\phi}$ notation refers to variables in the shifted field, not an average.

2.4 Noise in Field Theory

An equation for the time development of the distribution of particles is obtained by taking the functional derivative (see e.g. [13])[†] of the Action \mathcal{S} with respect to the complex field $\bar{\phi}$. Conversely, the equation for $\bar{\phi}$ is obtained by functional derivation of the Action with respect to ϕ , which often gives a pathological equation for $\bar{\phi}(t)$. It is however possible to remove $\bar{\phi}$ from the stochastic PDE for ϕ when the Action is quadratic in $\bar{\phi}$, by linearising the Action in $\bar{\phi}$. To do this we introduce an auxiliary field η , which will correspond to a noise field. To see why $\eta(\mathbf{x}, t)$ is a noise field, consider a single point in the field. Suppose η is Gaussian, uncorrelated noise[‡] with unit variance such that $\langle \eta(\mathbf{x}, t), \eta(\mathbf{x}', t') \rangle = \delta(\mathbf{x} - \mathbf{x}', t - t')$ and $p(\eta(\mathbf{x}, t)) = e^{-\eta^2/2}/\sqrt{2\pi}$, then the Fourier transform of this

[†]Note that this is the reverse of the standard method to obtain a field theory from a stochastic PDE representation [15], and is simple to do in practice.

[‡]Many authors prefer to incorporate the variance and correlations into the noise, defining correlators $\langle \eta(\mathbf{x}, t), \eta(\mathbf{x}', t') \rangle$ that absorb *all* noise terms and their cross-correlations, which is the appropriate form for further calculations. For clarity, we instead keep the noises simple and retain the explicit magnitudes, but must be careful to combine the noise terms for calculations.

240 is:

$$\frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} e^{-\eta^2/2} e^{-i2\pi k\eta} d\eta = e^{-2\pi^2 k^2}. \quad (16)$$

241 Therefore, by writing $q = \sqrt{2\pi}k$:

$$e^{-q^2} = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} e^{-\eta^2/2} e^{-i\sqrt{2}q\eta} d\eta. \quad (17)$$

242 We can equate q with (a convenient form of) the field $\bar{\phi}$ at a particular point
 243 (\mathbf{x}, t) . For example the final term in Eq. (14) is of the form $-a\bar{\phi}^2\phi$ (and H
 244 appears with an additional $-$ sign), so we can identify $q = \bar{\phi}\sqrt{-a\phi}$ and the
 245 term translates with noise to $\bar{\phi}\sqrt{2a\phi}\eta$, where η is Gaussian uncorrelated noise.
 246 In this sense, the field $\exp(-\bar{\phi}^2)$ represents the ‘integrated out’ form of the noise.

247 We proceed to calculate the linearised version of the noise for the above
 248 problems, with terms appearing in the formalism as $\exp(-H)$. We can replace
 249 the form q^2 with $-i\sqrt{2}q\eta$ in S , which if q is already in the form $\bar{\phi}^2$ will give us
 250 the result immediately, or we can rearrange the result by parts. If q^2 is negative
 251 (i.e. the original term was negative in H), this will lead to a real noise term,
 252 and conversely an imaginary noise term if q^2 is positive. Firstly, we rearrange
 253 one noise term found in Eq. (14) using integration by parts into an appropriate
 254 form:

$$-D\bar{\phi}\phi\nabla^2\bar{\phi} = -(D/2)\bar{\phi}^2\nabla^2\phi + D\phi(\nabla\bar{\phi})^2. \quad (18)$$

255 Noise terms normally cannot be decomposed without consideration of cross-
 256 correlations. Explicit consideration of correlations is complicated in this case as
 257 the $\bar{\phi}$ term appears within a gradient operator in some terms, but not in oth-
 258 ers. Fortunately, we can perform decomposition to real and imaginary parts;
 259 although care must be taken [16] to determine the relative importance of com-

260 bined real and imaginary noises, we can separate the real components (i.e. neg-
 261 ative terms in H) and imaginary components (i.e. positive terms in H) in Eq.
 262 (14) using Eq. (18):

$$H(\phi, \bar{\phi}) = D \int d^d x \left[-\bar{\phi} \nabla^2 \phi + \phi (\nabla \bar{\phi})^2 - \bar{\phi}^2 \left(\frac{\nabla^2 \phi}{2} + \frac{2}{p_m} \phi \right) \right]. \quad (19)$$

263 Since the noise terms appear as $\exp(-H)$, so are the opposite sign to how they
 264 appear in H , they transform as follows:

$$\begin{aligned} -D\phi(\nabla \bar{\phi})^2 &\rightarrow i\sqrt{2D\phi} \nabla (\bar{\phi})\eta \\ &\rightarrow -i \nabla (\eta\sqrt{2D\phi})\bar{\phi} \end{aligned} \quad (20)$$

$$D\bar{\phi}^2 \left(\frac{\nabla^2 \phi}{2} + \frac{2}{p_m} \phi \right) \rightarrow \sqrt{D(\nabla^2 \phi + \frac{4}{p_m} \phi)} \bar{\phi} \eta. \quad (21)$$

265 Eq. (21) also appears in the equation for the real noise from Eq. (15), using the
 266 $n = 2$ term from the sum; the translation to a noise field is only valid when the
 267 remaining sums are discarded as there would be correlations to consider with
 268 the higher order terms. Additionally, the imaginary Eq. (20) term is absent
 269 as the ρ field is constructed to be strictly real. Also, we will later need the
 270 linearised form for the $\bar{\phi}^2 \phi$ term:

$$\frac{2D}{p_m} \phi \bar{\phi}^2 \rightarrow 2\sqrt{\frac{D\phi}{p_m}} \bar{\phi} \eta. \quad (22)$$

271 The above fields can be simply described. Eq. (20) represents so called ‘diffusive’
 272 noise (in the imaginary axis, for our case) - it is conserved (the differential
 273 ensures that what goes in at one point comes out at the next) and decays
 274 with ϕ as $\sqrt{\phi}$ (recall $\langle \phi \rangle = \langle n(\mathbf{x}, t)/N \rangle$). Eq. (22) describes ‘square-root’ (in

275 magnitude) multiplicative noise. Because it is non-conservative, multiplicative
 276 noise in general can have dramatic effects on the behaviour of the system. We
 277 call Eq. (21) ‘mutation noise’, as it arises from movement only on a mutated
 278 birth event.

279 Representation of mutation noise as a stochastic PDE must be done carefully,
 280 as the term inside the square root may become negative when the gradient is
 281 large and negative. This is not physical and is due to representing the evolution
 282 process as continuous field theory, then forcing the field theory into a stochastic
 283 PDE. Consider the discrete representation of the term inside the square root in
 284 Eq. (21):

$$\nabla^2 \rho(\mathbf{x}, t) + \frac{4}{p_m} \rho(\mathbf{x}, t) = \rho(\mathbf{x} + 1, t) + \rho(\mathbf{x} - 1, t) + \left(\frac{4}{p_m} - 2 \right) \rho(\mathbf{x}, t). \quad (23)$$

285 This is *positive definite* since $p_m \leq 1$. We therefore impose the extra constraint
 286 that $\rho(\mathbf{x} + 1, t) + \rho(\mathbf{x} - 1, t) > \nabla^2 \rho(\mathbf{x}, t) > -2\rho(\mathbf{x}, t)$ on mutation noise. This
 287 can be achieved by using $\Theta(\nabla^2 \rho(\mathbf{x}, t) + 2\rho(\mathbf{x}, t))$, where $\Theta(y)$ is the Heaviside
 288 step function; $\Theta(y) = 0$ for $y \in (-\infty, 0)$ and $\Theta(y) = 1$ for $y \in (0, \infty)$. This
 289 ensures positivity but the convergence properties as $\Delta \mathbf{x} \rightarrow 0$ are not currently
 290 known.

291 2.5 Dimensional Analysis

292 In order to establish which terms are important for the ‘large scale’ behaviour
 293 of the system, dimensional analysis can be used. This involves considering the
 294 contribution of terms at different scales by assigning dimensions to the con-
 295 stants (called coupling constants) of each term, and ensuring that the equations
 296 are dimensionally consistent. The system is then rescaled and the constants
 297 will change according to their dimensions. We consider the ‘long wavelength’

298 limit, so that distance scales are much longer than any lattice spacing and the
 299 ‘fine structure’ is averaged out. The fine structure of models will depend on
 300 details such as the definition of the lattice and the exact form of mutations (i.e.
 301 whether strictly nearest neighbour or with some short ranged distribution such
 302 as exponential). Fine structure is lost in the dimensional rescaling, but many
 303 models have the same phenomenological description, i.e. are described identically
 304 at the macroscopic scale of large wavelengths. Thus the rescaling can result
 305 in significantly simpler models in which only the most important details are
 306 retained.

307 The following results will hold in the asymptotic limit of large population
 308 N , and apply only to the description at large scales. For all finite N there will
 309 be a clustering length scale. Together with κ , there would be two length scales
 310 in the problem and the appropriate dimensions for the coupling constant cannot
 311 be uniquely determined, hence dimensional analysis cannot be applied.

312 As all terms in the Action S given by Eq. (10) appear in an exponential
 313 (in Eq. (11)) they must be dimensionless. We define a wavevector $\kappa = h^{-1}$
 314 as our unit of measurement (with h a small length scale). Each term in the
 315 Hamiltonian H contains an integral of dimensions $\kappa^{-d}t^{-1}$ (d is the dimension of
 316 space), hence each term must have a spatial dimension of κ^d and time dimension
 317 t . Scaling of space will extract the relative importance of the terms in H ; time
 318 scaling must then be performed to ensure that the equation retains the time
 319 derivative term in the Action S with the dominant term(s) from H . The time
 320 scaling is not of interest in this case and we will not consider it further.

321 There is an arbitrary choice when defining the dimensions of ϕ and $\bar{\phi}$, pro-
 322 vided that $[\phi\bar{\phi}] = \kappa^d$; however, there is a ‘natural’ choice, meaning a choice in
 323 which the scaling dimensions of the terms is correct. We will identify the nat-
 324 ural choice for our case in Section 2.6, but progress can still be made without

325 assuming a particular dimensionality of ϕ as some terms are irrelevant in the
 326 limit $\kappa \rightarrow \infty$ regardless of the dimensional assignment.

327 We will be rescaling to large κ , and hence only the highest order terms
 328 in κ are ‘relevant’, as they will dominate the effective equation at large κ .
 329 We consider D dimensionless, but introduce a coupling constant on all terms
 330 that contains all dimensional components; this constant has magnitude 1 in the
 331 original, unscaled system. The derivative ∇ has scaling dimension $[\nabla] = \kappa^1$.
 332 The dimension of the fields are $[\phi] = \kappa^{d-\epsilon}$ and $[\bar{\phi}] = \kappa^\epsilon$, where ϵ is the parameter
 333 that controls the relative dimensions of the field and must be in $[0, d]$.

334 We proceed with an analysis of the dimensions of the coupling constants.
 335 Performing the full Renormalisation Group analysis [4] would explicitly perform
 336 the rescaling, providing details of how the scaling occurs and giving the natural
 337 choice of ϵ as a by product. We don’t perform this analysis, but instead consider
 338 all possible values of ϵ for now, and use previous results to identify the correct
 339 choice. The coupling constants introduced will be called a_i , where i is just a
 340 label. The terms of interest in $H(\phi, \bar{\phi})$ from Eq. (14) are:

$$\begin{aligned} [a_1 \bar{\phi} \nabla^2 \phi] &= \kappa^{d+2} [a_1] = \kappa^d \\ \implies [a_1] &= \kappa^{-2}, \end{aligned} \tag{24}$$

$$\begin{aligned} [a_2 \phi \bar{\phi} \nabla^2 \bar{\phi}] &= \kappa^{2+d+\epsilon} [a_2] = \kappa^d \\ \implies [a_2] &= \kappa^{-2-\epsilon}. \end{aligned} \tag{25}$$

$$\begin{aligned} [a_3 \bar{\phi}^2 \phi] &= \kappa^{d+\epsilon} [a_3] = \kappa^d \\ \implies [a_3] &= \kappa^{-\epsilon}, \end{aligned} \tag{26}$$

341 Recalling that $\epsilon \in [0, d]$, hence $\kappa^{-\epsilon} \geq \kappa^{-d}$, we can conclude the following.
 342 If we assume $\epsilon = 0$, then Eq. (26) dominates both Eq. (24) and Eq. (25).
 343 If we instead assume $\epsilon > 0$, then Eq. (24) dominates Eq. (25), although the
 344 importance of the remaining terms cannot be determined without knowledge
 345 of ϵ . Therefore the term $\phi \bar{\phi} \nabla^2 \bar{\phi}$ from Eq. (25) can be discarded, and the
 346 Hamiltonian H_0 for infinite N can be written:

$$H_0(\phi, \bar{\phi}) = \int d^d x \left[-D \bar{\phi} \nabla^2 \phi - \frac{2D}{p_m} \bar{\phi}^2 \phi \right]. \quad (27)$$

347 Some of these terms are also present in $H(\rho, \tilde{\rho})$, but there are additional terms
 348 that appear when considering the sums in Eq. (15), where we have the minimum
 349 summand variables $m = n = 2$ in the following terms:

$$\begin{aligned}
 [b_m \tilde{\rho}^{2m} \rho] &= \kappa^{d+2(m-1)\epsilon} [b_m] = \kappa^d \\
 \implies [b_m] &= \kappa^{-(2m-1)\epsilon}.
 \end{aligned} \quad (28)$$

$$\begin{aligned}
 [c_n \tilde{\rho}^n \nabla^2 \rho] &= \kappa^{2+d+(n-1)\epsilon} [c_n] = \kappa^d \\
 \implies [b_n] &= \kappa^{-2-(n-1)\epsilon},
 \end{aligned} \quad (29)$$

350 Hence we cannot yet truncate the exponential as all terms *may* be important,
 351 as they only scale negatively for certain values of ϵ . However, in the case $\epsilon >$
 352 0 then the real field ρ rescales to the same equation as the complex field ϕ ,
 353 i.e. $H_0(\rho, \tilde{\rho}) = H_0(\phi, \bar{\phi})$. Eq. (27) then provides the correct description of
 354 evolution in the infinite population limit. At large but finite N the importance of
 355 terms will correspond to their scaling dimension and hence we can make various
 356 levels of approximation in order to capture these details. The approximate

Hamiltonian for the real density is obtained from Eq. (15) by considering the first order correction to Eq. (27), given by the $n = 2$ term from Eq. (29):

$$H_1 = \int d^d x \left[-D\tilde{\rho} \nabla^2 \rho - \frac{D}{2} \tilde{\rho}^2 \left(\frac{\nabla^2 \rho}{2} - \frac{2D}{p_m} \rho \right) \right]. \quad (30)$$

2.6 Stochastic PDEs

A stochastic PDE can sometimes be obtained from the field theory by calculating the functional derivative of the Action S , as discussed in Section 2.4. This is possible when all terms can be linearised, and we have presented such Hamiltonians at various levels of approximation. Other Hamiltonians that cannot be made bilinear in the fields, such as Eq. (15) will not yield a stochastic PDE and will not be considered here. However, the available forms are the most important, consisting of: 1. Eq. (19), the exact equation for the evolution of the complex field ϕ . 2. Eq. (27), valid for ϕ in the infinite population limit, and we will find also valid for the real density ρ . 3. Eq. (30), the first order correction at large but finite population for the real density ρ .

The complete Hamiltonian $H(\phi, \bar{\phi})$ from Eq. (14) is rearranged to Eq. (19), which transforms with noise via Equations (20) and (21) to:

$$H(\phi, \bar{\phi}, \eta) = \int dx \left[-D\bar{\phi} \nabla^2 \phi - \sqrt{D \nabla^2 \phi + \frac{4D\phi}{p_m} \bar{\phi} \eta_1 + i\bar{\phi} \nabla (\eta_2 \sqrt{2D\phi})} \right]. \quad (31)$$

The two noise fields $\eta_1(\mathbf{x}, t)$ and $\eta_2(\mathbf{x}', t')$ are uncorrelated with unit variance, and form the real and imaginary parts of the noise with the given magnitudes. Therefore considering the full action S and taking the functional derivative with respect to $\bar{\phi}$, we obtain the stochastic PDE for the complex field in the evolution case:

$$\frac{\partial \phi(\mathbf{x}, t)}{\partial t} = D \nabla^2 \phi + \sqrt{D \nabla^2 \phi + \frac{4D\phi}{p_m} \eta_1 + i \nabla (\eta_2 \sqrt{2D\phi})}. \quad (32)$$

377 This equation is valid at arbitrary population size N , and is an exact representation
 378 in the sense that it captures the finite population size effects correctly (N
 379 appears via the density $\phi(\mathbf{x}, t) = n(\mathbf{x}, t)/N$). The only approximation involved
 380 is the use of continuous time and space, but the same ‘amount of individual’
 381 will be moved in a time unit as in the discrete case, with equal variance in both
 382 space and time.

383 Similarly, the best possible stochastic PDE for the real density in evolution
 384 is obtained from Eq. (30):

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = D \nabla^2 \rho(\mathbf{x}, t) + \sqrt{D \left(\nabla^2 \rho(\mathbf{x}, t) + \frac{4\rho(\mathbf{x}, t)}{p_m} \right)} \eta(\mathbf{x}, t), \quad (33)$$

385 with the added constraint that $\nabla^2 \rho(\mathbf{x}, t) > -2\rho(\mathbf{x}, t)$. The ‘mutation noise’
 386 appears because our individuals only ‘move’ when they reproduce, rather than
 387 diffusing throughout their lifetimes. We have to introduce a cutoff in the gradient
 388 to ensure that the mutation noise remains real.

389 Finally, we will show that only the square-root noise is ‘relevant’ in the
 390 infinite population limit, both for the real density ρ and the complex field ϕ , so
 391 in this case, $\phi = \rho$. The stochastic PDE obtained in this case from Eq. (27) is:

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = D \nabla^2 \rho(\mathbf{x}, t) + \sqrt{\frac{4D\rho(\mathbf{x}, t)}{p_m}} \eta(\mathbf{x}, t), \quad (34)$$

392 which is the equation for a birth/death process in which individuals diffuse in
 393 *real* space, given by Eq. (1).

394 We complete the analysis with the deduction of the dimensions of ϕ using ϵ
 395 and hence justify our claim that $d_c = 2$ and hence that the real space birth/death
 396 process is equivalent in the infinite limit to the evolution process.

- 397 1. The full evolution equation for the complex field ϕ , given by Eq. (14),
398 is dimensionally dominated by either ‘square-root’ noise or diffusion de-
399 pending on d , and therefore we can take the large wavelength, infinite
400 population limit and obtain the Hamiltonian for this process given by Eq.
401 (27), hence the stochastic PDE given by Eq. (34).
- 402 2. Eq. (34) is the same as Eq. (1) from Super-Brownian Motion in all dimen-
403 sions. Hence we can establish that $d_c = 2$ as in Super-Brownian motion,
404 and by combining Equations (24) and (26) for the dimensions of the de-
405 terministic diffusion term and the square-root noise term respectively, we
406 find that $\epsilon = d$.
- 407 3. Therefore the real field described by Eq. (15) can also be described by
408 Eq. (27) in the large population limit, as the truncation of the extra
409 terms present in the real field is now justified, as each is dimensionally
410 less important in $d \geq 1$ than the terms retained (from Equations (28) and
411 (29)).
- 412 4. Finally, by considering the terms that decrease less quickly with κ , the
413 stochastic PDE representing the leading order (large but finite N) correc-
414 tion to Eq. (27) is given by Eq. (30).

415 2.7 Numerical simulation of the stochastic PDEs

416 We have obtained approximate stochastic PDEs (alternatively, called Langevin
417 equations) for evolution (Equations (32), (33) and (34)) and argued that the
418 mutation noise term reduces to simple $\sqrt{\phi}$ noise in the large N limit. We also
419 have an exact equation for the complex field ϕ , which can be related to the real
420 density distribution. This is done by noting that in operator notation, operators
421 can be reordered by using the permutation relation so that it is ‘normal ordered’

422 (i.e. all \hat{a}^\dagger are to the left of all \hat{a}). The average of a normal ordered operator
 423 is identical to the average of the same operator with the \hat{a}^\dagger operators removed
 424 [4]; that is, $\langle (\hat{a}^\dagger)^m f(\hat{a}) \rangle = \langle f(\hat{a}) \rangle$. We can normal order operators by using the
 425 commutation relation, remove the \hat{a}^\dagger operators and then take the continuous
 426 limit as before. Therefore:

$$\langle \rho \rangle = \langle \hat{a}^\dagger \hat{a} \rangle = \langle \hat{a} \rangle = \langle \phi \rangle, \quad (35)$$

$$\langle \rho^2 \rangle = \langle \hat{a}^\dagger \hat{a} \hat{a}^\dagger \hat{a} \rangle = \langle \hat{a}^\dagger (\hat{a} + \hat{a}^\dagger \hat{a}) \rangle = \langle \phi \rangle + \langle \phi^2 \rangle. \quad (36)$$

427 Continuation to arbitrary moments is straightforward; each only depends on
 428 previous moments. Therefore, if we can calculate (or simulate from an exact
 429 equation) the moments of the complex field ϕ , we can calculate the moments of
 430 the real density exactly.

431 The final problem is of iterating a stochastic partial differential equation,
 432 although this is not a trivial task. We use the ‘splitting’ method presented
 433 in [17, 18, 19] to accurately numerically integrate the stochastic PDE, where
 434 possible. This method guarantees to give the correct results for the square-root
 435 noise term, but other terms can cause problems; in particular, $\phi = 0$ is supposed
 436 to be an absorbing state and it should be an attractor. The simplest approach of
 437 using Gaussian noise multiplied by dt directly changes $\phi = 0$ from an absorbing
 438 state to an unstable steady state, with probability 0 of finding it at any finite
 439 dt . The numerical solution of the $\Delta_t \phi(\mathbf{x}, t) = \sqrt{\frac{D}{2}} \nabla^2 \phi + \frac{4\phi}{p_m} \eta(\mathbf{x}, t)$ term does
 440 not seem have an algorithm for finite dt in the literature and so we use ad-hoc
 441 truncation to zero as described in Section 2.4, though it should be noted that
 442 pursuing numerical integration is dangerous in this case.

443 2.7.1 Numerical results

444 We now present the results of simulating the partial differential equations ob-
 445 tained for the diffusion case and the approximated evolution case, and show
 446 that they behave approximately as expected. For comparison purposes, we also
 447 show the behaviour the stochastic PDE obtained from a simple diffusion of N
 448 non-interacting particles (see Appendix A):

$$\frac{\partial \rho_D(\mathbf{x}, t)}{\partial t} = D \nabla^2 \rho_D(\mathbf{x}, t) + \nabla(\eta(\mathbf{x}, t) \sqrt{2D\rho_D(\mathbf{x}, t)}). \quad (37)$$

449 Note the presence of the ∇ on the noise term, ensuring that this noise conserves
 450 particles locally. Figure 2 (Left) shows the general behaviour of the distributions
 451 for Eq. (34), containing only square root noise and corresponding to the ‘real
 452 space’ case of reproducing and dying particles subject to spatial diffusion. The
 453 Figure demonstrates that square root noise does produce clustering and permits
 454 local and global extinction. However, we find that Eq. (34) only captures the
 455 qualitative aspects of the clustering. Figure 2 (Right) shows the (ensemble aver-
 456 aged) Interface Width[§] of the distribution against time, comparing the various
 457 cases. We compare all of the stochastic PDEs we have encountered, and see
 458 that all terms are important quantitatively - the width is not correctly repre-
 459 sented in any approximation, even at this fairly large value of $N = 10000$. The
 460 diffusion stochastic PDE (Eq. (37)) fits the Master Equation solution (Eq. (7)
 461 from [4]) closely. Only diffusion and square root noise can be guaranteed to be
 462 accurate numerical integrations of the corresponding stochastic PDEs, due to
 463 the numerical problems discussed above. The average interface width increases
 464 with time after passing some minimum value in all evolution cases, because the
 465 total population is not conserved. Since we disregard runs in the ensemble av-

[§]The Interface Width $\langle n(x)^2 \rangle - \langle n(x) \rangle^2$ is *not* directly related to the standard deviation of the distribution, but rather the distribution is viewed as an interface. The Interface Width describes the ‘roughness’ or deviation of the distribution from a straight line.

466 erage where the population becomes extinct the average population size tends
 467 to increase from its initial value[7].

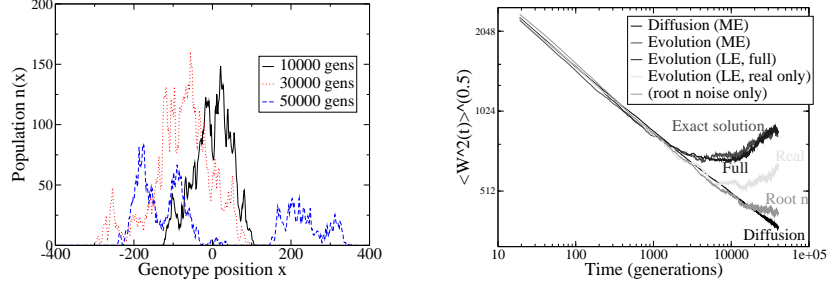


Figure 2: Left: Evolved population distribution for the evolution case using the approximation of infinite N , given by Eq. (34). Shown is the distribution at various times. Note that it allows the distribution to split into multiple clusters as the original Master Equation, and local extinction is possible. Qualitatively, the model appears accurate. Right: Interface width $\langle n(x)^2 \rangle - \langle n(x) \rangle^2$ as a function of time for the various relevant cases, with initial conditions of all population starting at position 0. Plotted are, from the bottom up, ‘1. Diffusion ME’: the Master Equation evaluation of Diffusion (Eq. (7) from [4]) which is indistinguishable on this plot from the diffusion stochastic PDE from Eq. (37). ‘2. Evolution (LE, root n noise only)’: given by (Eq. (34)). ‘3. Evolution (LE, real only)’: the full solution given by Eq. (32) with the insistence that the field is real (truncation of negative densities to 0). ‘4. Evolution (LE, full)’: the full solution (Eq. (32)) itself. Finally, ‘5. Evolution (ME)’: the Master Equation evaluation of evolution (Eq. (2)). Only the full consideration of the complex solution yields the desired behaviour, although the qualitative dynamics of a peak are captured. We use $D = 0.25$ and $N(t = 0) = 10000$ throughout.

468 The full complex solution from Eq. (32) quantitatively captures the dynam-
 469 ics, although it must be admitted that the ‘ad-hoc’ nature of the process for
 470 discretisation permits us to try different procedures and keep only those that
 471 worked. This successful regime used a truncation of densities under a small
 472 amount chosen specifically for the time-step and total population, and the time-
 473 step was chosen very small. Gaussian numbers were used for the generation of
 474 the noises.

475 **3 Summary**

476 We found that death and reproduction with mutation in a type space is iden-
477 tically described in the large scale and population limit as diffusing particles
478 undergoing birth/death processes, and is therefore described by a super Brown-
479 ian Motion. This tells us that the critical dimension for the evolution process is
480 2 in Euclidean space. Hence specialised models such as presented in [1] are es-
481 sential for considering the distribution of a given phenotype ($d \leq 2$). In higher
482 dimensions $d > 2$ lineage analysis is sufficient to describe the distribution of
483 types developing in time, when coupled with the representation of type space.
484 However, all cases require a microscopic consideration of the underlying process
485 for calculations at finite N . Our simple Field Theory analysis has provided an
486 exact description of the problem in the form of a stochastic PDE, Eq. (32).

487 We found the first order correction to the infinite N stochastic PDE, given
488 by Eq. (33). This is valid when the total population N is large but finite. Ob-
489 taining the correct stochastic PDE to represent a microprocess is non-trivial and
490 mistakes are often made, as discussed in Ref. [16], and hence a careful deriva-
491 tion such as ours is very important. Our work brings together previous results
492 and makes the underlying clustering process in evolution explicit. Field theory
493 is a tool that permits examination of finite systems and our work discusses the
494 relevancy of stochastic PDEs in this case.

495 **Acknowledgements**

496 DJL acknowledges the EPSRC and the Scottish Government for funding, as well as
497 Imperial College London where some of this research was carried out. We are very
498 thankful to Martin Howard and Uwe C. Täuber for invaluable discussions on the
499 method.

500 A Calculating the Stochastic PDE for Diffusing 501 particles

502 The starting point for diffusion is the Action for diffusing and non-interacting particles,
503 obtained from Eq. 35 in [4] for diffusing interacting particles, by setting the reaction
504 rate λ_0 to zero:

$$A_d(\phi, \tilde{\phi}) = \int d^d x \int dt \left[\tilde{\phi} \partial_t \phi - D \tilde{\phi} \nabla^2 \phi \right]. \quad (38)$$

505 Here we have also neglected terms for initial and final conditions. We first convert to
506 a real density field ρ using the methods from Section 2.3, by setting $\phi = \rho e^{-\tilde{\rho}}$ and
507 $\tilde{\phi} = e^{\tilde{\rho}}$. In this case the exponential terms cancel out and we are left, after integration
508 by parts, with:

$$A_d(\rho, \tilde{\rho}) = \int d^d x \int dt \left[\tilde{\rho} \partial_t \rho - D \tilde{\rho} \nabla^2 \rho + D \rho (\nabla \tilde{\rho})^2 \right]. \quad (39)$$

509 The final noise term is linearised using Eq. (20) with but is of opposite sign, therefore
510 giving the linearised Action:

$$A_d(\rho, \tilde{\rho}, \eta) = \int d^d x \int dt \left[\tilde{\rho} \partial_t \rho - D \tilde{\rho} \nabla^2 \rho + \nabla(\eta \sqrt{2D\rho}) \tilde{\rho} \right], \quad (40)$$

511 which on functional differentiation with respect to $\tilde{\rho}$ yields Eq. (37).

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